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From ozone depletion to agriculture: understanding the role of UV radiation in sustainable crop production

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Summary

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Largely because of concerns regarding global climate change, there is a burgeoning interest in the application of fundamental scientific knowledge in order to better exploit environmental cues in the achievement of desirable endpoints in crop production. Ultraviolet (UV) radiation is an energetic driver of a diverse range of plant responses and, despite historical concerns regarding the damaging consequences of UV-B radiation for global plant productivity as related to stratospheric ozone depletion, current developments representative of a range of organizational scales suggest that key plant responses to UV-B radiation may be exploitable in the context of a sustainable contribution towards the strengthening of global crop production, including alterations in secondary metabolism, enhanced photoprotection, up-regulation of the antioxidative response and modified resistance to pest and disease attack. Here, we discuss the prospect of this paradigm shift in photobiology, and consider the linkages between fundamental plant biology and crop-level outcomes that can be applied to the plant UV-B response, in addition to the consequences for related biota and many other facets of agro-ecosystem processes.

‘A recognition of the balance and interactions between genotype, environment and management is the intelligent solution to feeding the growing global population.’

(Porter & Wollenweber, 2010)

I. Introduction

The world is currently faced with a grand challenge of feeding larger numbers of people with increasingly restrained resources. Closing the growing ‘yield gap’ in global food crop production is

key to surmounting the obstacles required to feed 9 billion people by 2050 (The Royal Society, 2009), yet our ability to mitigate the increased food requirements on a global scale is likely to become significantly constrained as a consequence of global climate change (Godfray *et al.*, 2010). The breadth of factors governing crop production is vast, but increasing our understanding of environmental influences on plants, incumbent ecosystems and global atmospheric processes represents a diverse, yet significant, component of our capability to maintain healthy, sustainable food sources into the future. In a similar manner to the historical study of the factors that can augment yield and crop quality parameters during cultivation, the possibilities presented by the 'smart acclimation' or priming of plants to yield-limiting stress conditions, in a manner which can pre-acclimatize plants to problematic encounters that may be met later in development, are now being explored in more detail. One key environmental factor is sunlight, which drives primary productivity via photosynthesis, but is also responsible for the supply of informational cues vital to plant development, cues to which plants have evolved highly perceptive responses over time. Ultraviolet (UV) radiation sits 'beyond the violet' component of the visible spectrum (< 400 nm) and is more energetic in nature than, for example, photosynthetically active radiation (PAR; 400–700 nm). Much of the life on Earth is inescapably exposed to UV radiation to some degree, particularly plants, and yet the possibilities to exploit biological responses to UV for agronomic gain remain largely unexplored, in part as a result of historical concerns regarding the damaging consequences of excess exposure to UV-B radiation (280–315 nm) for many forms of life on Earth with the loss of stratospheric ozone (Farman *et al.*, 1985; Caldwell *et al.*, 2003; Norval *et al.*, 2007). The international response to ozone depletion was the Montreal Protocol, which was implemented in 1989, and subsequently led to a rapid decline in the use of chlorofluorocarbons (CFCs), with the recent beginnings of a recovery of stratospheric ozone evident in certain locations, thought to be a consequence of the declining use of ozone-depleting substances (Steinbrecht *et al.*, 2009). However, there is still inherent uncertainty regarding the future levels of UV-B radiation, and the possible impacts of climate change on the global UV environment in the near and longer term future are still not well understood (Rex *et al.*, 2006; Hegglin & Shepherd, 2009; Watanabe *et al.*, 2011; Andrady *et al.*, 2012). UV radiation is also dynamic across a variety of spatial scales; for example, UV-B fluxes increase with increasing altitude and decreasing latitude, except in proximity to areas of ozone depletion at lower latitudes (McKenzie *et al.*, 2006), and can also be influenced by surface conditions, such as albedo and snow cover (Koepke & Mech, 2005). It is also well established that UV-B levels vary between hemispheres, with some sites in the Southern hemisphere receiving up to twice the UV observable at a comparable latitude in the Northern hemisphere (Seckmeyer *et al.*, 2008). Indeed, such a north–south 'divide' is particularly important when considering the increasing contribution of Southern hemisphere countries to global food production (www.fao.org). Thus, despite the past and recent successes in limiting CFC-driven stratospheric ozone loss, there is still little certainty regarding incident UV-B

levels during the remainder of the century, and many locations on Earth remain exposed to relatively high UV-B irradiances regardless. Largely as a result of the concerns regarding the consequences of ozone depletion, a diverse range of responses to UV radiation have been observed in many plants and other organisms, many of which are frequently species of agricultural importance. Here, we discuss the evolving paradigm shift which an enhanced understanding of the effects of UV radiation within the context of food production could now present. Specifically, we consider the technologies, barriers and advances in fundamental multidisciplinary science which may further enhance the knowledgeable exploitation of UV radiation in the future.

II. UV radiation can drive beneficial endpoints in crop production

1. Agricultural resilience and UV photomorphogenesis

Since the Green Revolution, there has been a steady increase in crop yields worldwide, achieved through the expansive use of various agrochemicals and fertilizers in addition to intensive breeding of high-yielding grains and other crop varieties (Zhu *et al.*, 2000; Evenson & Gollin, 2003). This observed increase in achievable yield has now begun to slow (Godfray *et al.*, 2010) and, with the global population continuing to grow, a great deal of attention is now focused on sustainable solutions to a perceived food supply problem. Although the possibilities to strengthen global food security via the use of genetic modification are significant (Jones, 2001; Paine *et al.*, 2005; Ren *et al.*, 2005), routes to make sizeable gains in crop production and quality also exist through the intensification of 'agricultural resilience' (Pretty, 2008), whereby the impact of damaging environmental stresses on crops are mitigated to as large an extent as possible. Furthermore, the growing threat of future climatic uncertainty heightens the risks posed to our increased ability to produce nutritious foodstuffs on a global basis (Easterling *et al.*, 2007; Morton, 2007; Lobell *et al.*, 2008). The concept of mitigating stress and/or optimizing environmental conditions to genotypic makeup and phenotypic character is of course not new, and there are numerous examples whereby a nonpassive approach to the management of plant response to environmental stimuli have indicated marked possibilities for crop improvement, including cultivar selection for root architectural plasticity for water and nutritional acquisition (Ho *et al.*, 2005), biofortification of crops for enhanced nutritional composition (White & Broadley, 2009), use of generalist strategies for cultivation improvement in challenging environments (Turner, 2004), enhanced cultivar–environment matching (Condon *et al.*, 2002) and targeting of traits for salinity tolerance in crops (Munns *et al.*, 2002). A related term is that of 'eustress' or positive stress, whereby the elicitation of a stress response provides a beneficial outcome for an organism (Mauch-Mani & Mauch, 2005; Ashraf & Foolad, 2007). Furthermore, the somewhat similar concept of 'priming' plants to maintain productivity when challenged with subsequent, greater levels of stress later in development could present a valuable tool in the sustainable management of crop protection in a range of environments (Beckers & Conrath, 2007).

Examples of approaches explored to date include the exogenous application of phytohormones to growing plants and seed (van Hulst *et al.*, 2006; Worrall *et al.*, 2012) and the use of partial root zone irrigation to enhance crop quality in a water-limited environment (Davies *et al.*, 2011). There are now arguably parallel possibilities for UV radiation to be exploited as a priming instrument in the enhancement of crop production, yet much previous debate has centred on the possible consequences for plant productivity due to the threat of increased UV-B levels via ozone losses (Tevini *et al.*, 1981; Caldwell *et al.*, 1995, 2003). Understanding the potential of UV radiation as a regulatory factor for enhanced food crop prosperity requires a brief overview of our current understanding of fundamental plant responses to UV, and there are now several well-established plant responses to UV radiation which we can consider.

Leaf expansion is invariably inhibited in response to UV radiation (González *et al.*, 1998; Ruhland & Day, 2000; Searles *et al.*, 2001) and, despite the evaluation of several mechanistic and regulatory candidates across many studies (e.g. Jansen, 2002; Potters *et al.*, 2007; Laxmi *et al.*, 2008; Wargent *et al.*, 2009b; Gruber *et al.*, 2010; Hectors *et al.*, 2010), an integrated model for UV-B leaf photomorphogenesis has not yet been resolved, should one exist. Additional elements of leaf UV morphogenesis that are often observed concomitant to reduced leaf size include increases in leaf thickness (Bornman & Vogelmann, 1991; Staxén & Bornman, 1994; Rozema *et al.*, 1997), and leaf mass per unit area (Sprtova *et al.*, 2003; Láposi *et al.*, 2009), accumulation of leaf surface waxes (Cen & Bornman, 1993), and reductions in plant total leaf number, as observed in crop species, such as *Cucumis sativus* and *Lactuca sativa* (Krizek *et al.*, 1997, 1998), a response which may be attributable to the cost of eliciting phenolic compounds to provide a measure of protection to plants. One question yet to be addressed is should we consider reduced leaf expansion as a negative outcome for crop productivity without exception? Equally, other related elements of leaf UV photomorphogenesis may actually provide a tool to produce more resilient crop plants.

Another key plant response to UV radiation is that of heightened secondary metabolism activity. It is clear that plants have proficiently adapted to produce 'sunscreening' compounds (e.g. flavonoids) when confronted with increased exposure to UV (as discussed in detail by Bassman, 2004), and that such responses may represent valuable cues in the exploitation of plant pigmentation in crop production (Krizek *et al.*, 1998). Both induced and constitutively produced accumulation of such compounds has been shown to reduce the penetration of UV wavelengths deeper into leaves, protecting photosynthetic machinery and other essential components from possible harm (Bornman & Vogelmann, 1991; Day *et al.*, 1993). What is somewhat less clear at present is: (1) the manner in which overall leaf metabolite composition is driven by discrete elements of both the UV-specific and generalized plant response, and (2) how different complexes of protective compounds can lead to differing outcomes for plant development and ensuing interactions with the surrounding environment, such as pest and pathogen attack in an agronomic environment. Equally, below-ground responses to UV radiation, as initiated by the above-ground plant phytochemical response, have received comparatively

little attention to date, but there are indications that alterations in biomass partitioning to roots and changes in root exudate release are sensitive to UV-B (Rinnan *et al.*, 2006).

Although such clear phenotypic changes in response to UV radiation are commonly observed outcomes, there is still limited understanding of the regulatory processes which govern many aspects of UV photomorphogenesis, particularly with regard to signal transduction and other early-stage responses to UV-B and UV-A radiation. Initial UV-B signalling events have been categorized by authors in a varied manner to date (as reviewed, in detail, by Jenkins, 2009); however, the prevailing distinction is often between high-flux, shorter wavelength UV-B responses (e.g. DNA lesion production) and lower flux signalling transduction pathways, which are often described as photomorphogenic in nature, and may be specific to defined UV-B signal transduction pathways. Although DNA is known to strongly absorb UV (Taylor *et al.*, 1996), plants are proficient in regulating flavonoid photoprotection to limit DNA damage (Stapleton & Walbot, 1994; Mazza *et al.*, 2000; Rozema *et al.*, 2002), and the photorepair of DNA lesions and other photoproducts is also rapidly initiated via photoreactivation processes (Jiang *et al.*, 1997). High-fluence, nonphotomorphogenic UV responses also appear to overlap with plant signalling modes which are commonly elicited in response to other challenges that plants routinely face, such as oxidative stress, herbivory and pathogen attack (Landry *et al.*, 1995; Rao *et al.*, 1996; Mackerness *et al.*, 1999a,b; Hideg *et al.*, 2002; Kalbina & Strid, 2006); however, we still know relatively little regarding the putative role of reactive oxygen species (ROS) as a component of the UV-B response under natural conditions (as discussed in detail by Hideg *et al.*, 2012). Overlaps between common defence pathways and UV-B signalling are not only complex, but also indicate that UV-B radiation may have a role as a valuable cue in regulating the responses of crop plants to the challenges presented by an ever-changing environment.

The knowledge of UV-B-specific responses often characterized as photomorphogenic in nature is now growing through the use of transcriptomic and genetic screening approaches in *Arabidopsis* (as reviewed, in detail, by Heijde & Ulm, 2012). The main focus of such studies has been on the identification of the regulatory components orchestrating typical phenotypic outcomes as a consequence of UV-B exposure, such as phenolic pigmentation (e.g. induction of precursor genes, such as *CHALCONE SYNTHASE (CHS)*) and inhibition of hypocotyl elongation (Kim *et al.*, 1998; Jenkins *et al.*, 2001; Suesslin & Frohnmeyer, 2003; Ulm & Nagy, 2005; Jenkins & Brown, 2007). Much recent attention has been focused on the identification of a UV-B-specific photoreceptor which may act as the primary chromophore for UV-B, in a similar regard to the receptors identified which respond to other wavelengths of light (e.g. Briggs & Christie, 2002; Franklin & Whitelam, 2004), and a suite of signal transduction components has been revealed. Key regulators of UV-B signal transduction include CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), which has been shown to regulate a range of low-fluence gene expression responses as mediated by UV-B wavelengths, in addition to subsequent flavonoid accumulation and inhibition of hypocotyl elongation (Oravec *et al.*, 2006), and the bZIP

transcription factor ELONGATED HYPOCOTYL 5 (HY5), which, much like COP1, is known to regulate several different photomorphogenic pathways (Osterlund *et al.*, 2000; Chen *et al.*, 2004), but is also required for UV-B-mediated gene expression (Ulm *et al.*, 2004; Brown *et al.*, 2005; Oravec *et al.*, 2006; Brown & Jenkins, 2008). Following the work of Kliebenstein *et al.* (2002), the UV-B-responsive UV RESISTANCE LOCUS 8 (UVR8) signalling component was identified, which has been shown to act solely in the UV-B-specific regulation of gene expression (Brown *et al.*, 2005). At the same time, at least two genetically distinct UV-B signalling pathways have been revealed in Arabidopsis, one of which requires UVR8 (Brown & Jenkins, 2008). Microarray analysis from several studies has indicated that UVR8 regulates the transcription of a broad range of genes in response to UV-B, but our understanding of the diverse roles of UV-B-specific signalling under varying conditions remains limited. Figure 1 provides a summary of the functional gene groups altered significantly in expression in response to UV-B exposure in wild-type plants and the *uvr8* mutant across two studies (Brown *et al.*, 2005; Favory *et al.*, 2009). Although the UV-B dose, as defined by the fluence rate, was somewhat different between the studies ($1.5\text{--}3.0\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$), the spectral composition of UV-B treatments also differed, that is, broad-band UV-B (280–320 nm) vs the use of a narrow-band UV-B source (*c.* 312 nm) combined with a cut-off filter, which confined the spectrum to wavelengths $> 305\ \text{nm}$. Those plants exposed to broad-band UV-B treatment initiated a range of different responses to those in the narrow-band experiment of Favory *et al.* (2009); the study by Brown *et al.* (2005) showed quite strong induction of various genes that are indicative of a rather acute response to UV-B treatment (Fig. 1), including extensive down-regulation of genes regulating photosynthetic processes, carbohydrate metabolism, cell wall development and cell cycle function. Interestingly, although many gene functional groups from the study of Brown *et al.* (2005) indicated a stronger fold response to UV-B in the *uvr8* mutant, wild-type plants from the same study also exhibited clear down- and up-regulation across several gene classes (e.g. photosystem constituents, biotic stress factors, phytohormones) and frequently in a parallel manner to *uvr8*. The narrow-band UV-B treatments imposed in the study of Favory *et al.* (2009) indicated generally more subtle responses (Fig. 1), yet certain strong overlaps with broad-band UV-B treatment could be observed across both wild-type and the *uvr8* mutant; for example, cell wall-related genes were strongly down-regulated in both wild-type and *uvr8* across all treatments, with the exception of the 1-h time point within the narrow-band UV-B treatment group. Conversely, although the narrow-band UV-B treatments led to the up-regulation of genes associated with phenylpropanoid metabolism in the wild-type, this up-regulation was absent from the broad-band UV-B-treated plants. Although plant age and other experimental conditions must be acknowledged when comparing the two studies, the probable difference in biologically effective UV radiation between broad-band, shorter wave treatments and longer wave, narrow-band UV treatments could certainly be a key diversifying factor between the studies, depending on the selected action spectrum used to weight UV dose (Flint & Caldwell, 2003). Equally, broad-band, higher fluence

UV-B treatments may be more likely to activate UVR8-independent genes; for example, González Besteiro *et al.* (2011) demonstrated that broad-band UV-B treatment initiated responses which did not involve UVR8 signalling. Furthermore, such acute response pathways can actively antagonize UV-B-specific photomorphogenic signalling (Ulm *et al.*, 2004). Such comparisons highlight not only the need to expand our understanding of UV-B photomorphogenesis to consider sunlight responses in the field, but also the fact that the regulatory influence of UVR8-mediated responses to UV-B extends beyond the induction of phenylpropanoid metabolism alone. In the search for a UV-B photoreceptor, Rizzini *et al.* (2011) demonstrated that UVR8 monomerizes in a UV-B-dependent manner before interaction with COP1, thus indicating that UVR8 is indeed a UV-B photoreceptor. The functional structure of UVR8 was then rapidly elucidated, describing a dimer dissociation response triggered by the absorption of UV-B via a series of tryptophan residues (Christie *et al.*, 2012; Wu *et al.*, 2012). These exciting advances in our understanding of UV-B perception have been heralded as providing significant opportunity for biotechnological progress (Gardner & Correa, 2012), and will probably now empower the exploitation of UV-B photomorphogenesis in species of agricultural importance more than ever before, for example, via manipulation of UVR8 constitutive or inducible expression within breeding programmes. Despite the fact that UV-B photoperception and signal transduction are now becoming better understood, we still know very little about the relative responses of the UVR8 network within the broad range of ambient UV environments in which many plants grow under field conditions. Although very few studies have characterized UVR8-related responses with the use of biologically weighted UV doses, there are indications that the acclimation afforded to plants by UVR8 extends across a wide range of biologically effective UV fluxes typically observed at many latitudes (Wargent *et al.*, 2009a). In terms of the UV-B phenotypic response, UVR8 has been shown to regulate aspects of the UV-B growth response, and may be a key player in the regulation of cellular development and growth in plants subjected to UV-B exposure (Wargent *et al.*, 2009a). In conclusion, the plant response to UV is often efficient, perceptive and enacted through a range of overlapping and nonrelated, accumulative processes from signal transduction to physiological perturbation. Such a diverse range of responses presents the tantalizing prospect that such phenomena can now be exploited to enhance agricultural outputs and, more specifically, improve crop productivity and nutritional quality, particularly following the recent elucidation of a UV-B-specific photoreceptor system.

2. UV radiation is rarely a damaging source of stress for plants

There is now overwhelming evidence that plants are not only proficient at regulating archetypal responses to UV radiation, but also that the exposure of plants to supplementary UV rarely leads to gross damage or any fundamental threat to a plant's survival. Indeed, it could be argued that UV radiation acts as a ubiquitous, albeit energetic, cue in the regulation of typical plant development, as opposed to a consistent inducer of damage. This concept has now

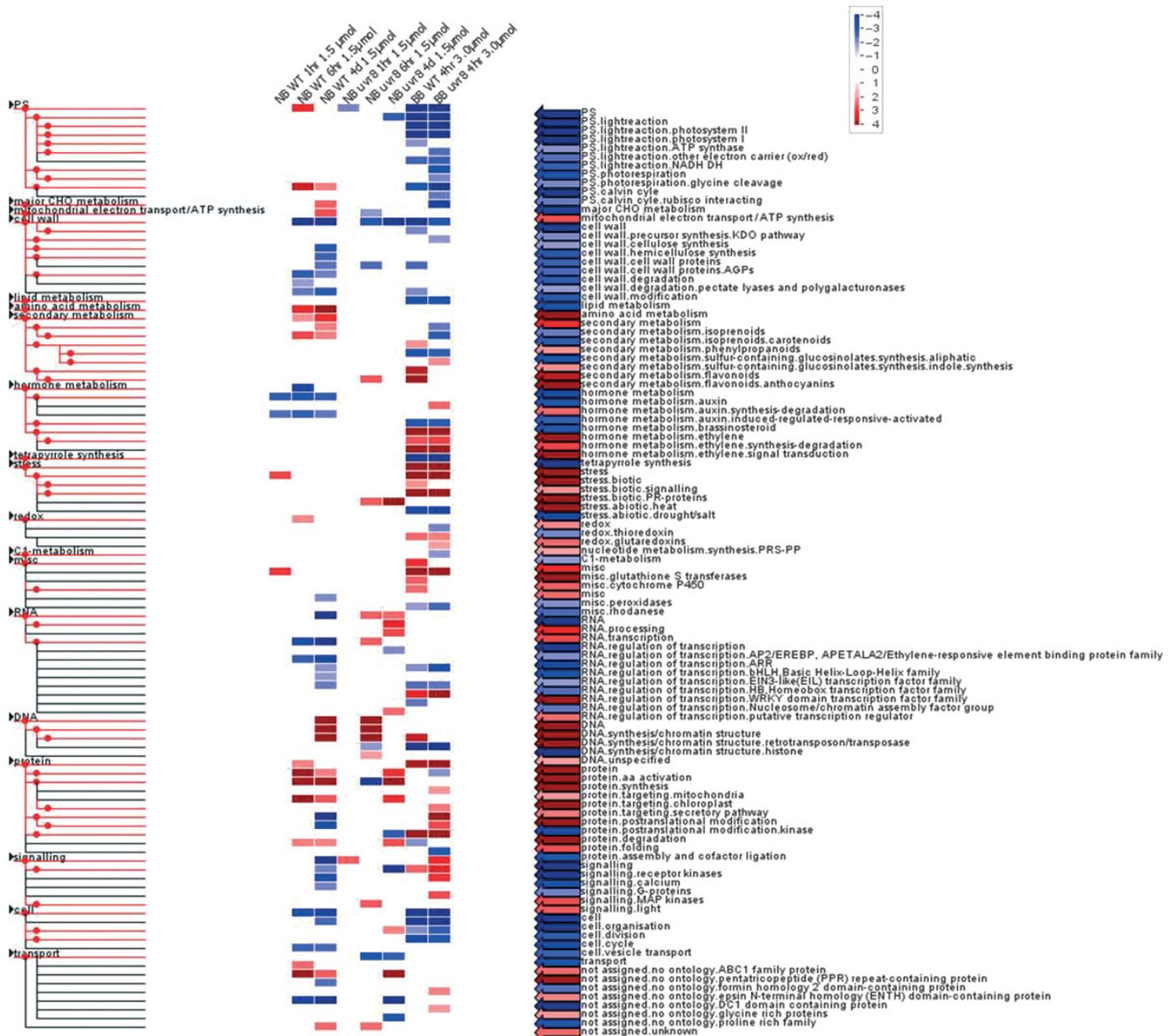


Fig. 1 UV-B plant response is diverse and dynamic. Summary of MapMan gene categories, as displayed by PageMan (Thimm *et al.*, 2004; Usadel *et al.*, 2006), representing relative transcriptomic responses to UV-B treatments. Microarray expression data from the studies of Favory *et al.* (2009; columns 1–6) and Brown *et al.* (2005; columns 7–8) were subjected to Wilcoxon rank sum testing within MapMan to identify significant differences in expression patterns within each functional gene group compared with each entire dataset per sample. Expression ratios are calculated on the basis of UV-B treatments according to genotype (*uvr8*; wild-type) compared with zero UV-B treatments (columns 1–3, WT; columns 4–6, 8, *uvr8*). Columns are also annotated according to duration (1 h, 4 h, 6 h, 4 d), nature of UV-B treatment (BB, broad-band treatment at 280–320 nm; NB, narrow-band treatment with peak output at c. 312 nm and cut-off of < 305 nm) and fluence rate in $\mu\text{mol m}^{-2} \text{s}^{-1}$. Coloured boxes indicate statistically significant groups (Benjamini & Hochberg-corrected *P* value below 0.05), and colour scale represents *z*-transformed *P* values, with red indicating a trend within the group for the up-regulation of expression relative to no UV-B controls, and blue indicating a trend within the group for down-regulation. Arrows, shown with the same colour scheme, indicate MapMan annotation of differentially regulated gene classes. Results from all Wilcoxon comparisons according to MapMan gene category for each treatment are given in Supporting Information Table S1.

been demonstrated by several studies and meta-analyses (e.g. Searles *et al.*, 2001; Hectors *et al.*, 2007); moreover, it has been argued that the vast majority of studies which have indicated chronic damage responses to UV-B have tended to employ unnaturally high UV fluxes (Allen *et al.*, 1998). It is also clear that the experimental approach is a significant influence on the nature

and magnitude of responses observed to date; for example, Newsham & Robinson (2009) analysed 34 studies of the UV-B response in Arctic and Antarctic bryophytes and angiosperms, and noted that attributes, such as the concentration of UV-B-absorbing compounds and above-ground biomass, were affected significantly by the deployment of UV screening filters, whereas those studies

analysed which used supplementary UV lamps were not shown to have a significant effect on these parameters. Although the sudden exposure of plants and related organisms to UV, often encountered in many experimental approaches, may not be viewed as realistically mimicking prolonged natural exposure conditions, many components of typical agricultural production processes are of a highly dynamic nature, with 'sudden' UV exposure events of young plants or harvestable components of mature plants (e.g. fruit) happening routinely across the agricultural landscape, indicating scope for the manipulation of responses to UV-B within common agronomic practice.

In terms of the plant physiological attributes which often characterize a quality marker for crop production, arguably the key attributes are the productivity or final harvestable growth and associated nutritional qualities. The demands of intensified food crop production exert a vast range of stresses on plant health in general, and photosynthetic capacity in particular, with mechanical, chemical and biological stimuli driving significant limitations in subsequent yield (Singh *et al.*, 2002; Chaves *et al.*, 2003; Mittler, 2006). Despite the work of Searles *et al.* (2001), there are a range of studies which have suggested damaging effects to the photosynthetic capability of a range of species as a consequence of UV-B exposure, particularly when spectral responses of components are characterized *in vitro* (Melis *et al.*, 1992; Vass *et al.*, 1996). Yet, authors have conversely shown that, in whole-plant systems exposed to UV-B doses in excess of the fluxes commonly observable in nature, few effects are observed (Middleton & Teramura, 1993; Nogués & Baker, 1995). In addition, there is some evidence that UV-B can impact upon those mechanisms driving carbon fixation (Jordan *et al.*, 1992; Allen *et al.*, 1997). However, the bulk of historical observations have arguably been made either in an isolated system or at comparatively high UV fluxes; indeed, Allen *et al.* (1998) pointed out that singular focus on a given photosynthetic component fails to take into account rate limitations imposed by additional photosynthetic reactions in a complete system. It is clear that, in assessing the realistic likelihood of negative impacts of UV-B on photosynthesis in the future, assessments of whole-plant alterations in response (e.g. changes in leaf morphology combined with the up-regulation of phenolic metabolism) will act as critical markers, as opposed to single-component effects as mediated by narrow-band or unrealistic wavelength exposures.

Of the related phenomena which may constrain plant productivity under stressful conditions, photoinhibition is arguably one of the most significant, whereby either a reversible or nonreversible light-dependent retardation of photosynthesis occurs, chiefly as a consequence of limitations within photosystem II (PSII) (Long *et al.*, 1994). In concordance with studies detailing negative impacts on photosynthesis, there are numerous studies indicating that UV can lead to reductions in the maximum photochemical efficiency of PSII, quantified as F_v/F_m (Teramura & Sullivan, 1994; Fiscus & Booker, 1995; Krause *et al.*, 2003; Takahashi *et al.*, 2010), indicating dynamic or chronic damaging effects on the competence of PSII. There are, however, indications that UV radiation is unlikely to induce gross damage under typical sunlight exposure and, moreover, that UV may play a prominent role in the photoprotection of the photosystem in a challenging environment.

For example, leaf discs of *Pisum sativum* and *Phaseolus vulgaris* pretreated with UV-B radiation exhibited a slower decline in F_v/F_m during exposure to high light (Bolink *et al.*, 2001), and some authors have suggested that the acclimative photoprotective effects of UV-B (e.g. leaf phenolic compounds, epidermal waxes) are likely to limit the corruption of photosystem competence (Hakala-Yatkin *et al.*, 2010; Wargent *et al.*, 2011). However, although the induction of UV-absorbing leaf phenolics may offer protection against photoinhibition, plant resource strategy theory and experimental observations suggest that secondary metabolite provision comes at a cost to constitutive plant productivity (Hofmann & Jahufer, 2011), a question which is certainly far from resolved with respect to UV-B response generally, and possible consequences for crop production in particular. In summary, there is burgeoning evidence to support the likelihood that chronic damaging effects of UV radiation on plant functionality are rarely observed in plants that are exposed to balanced, nonmonochromatic, realistic fluxes of UV; moreover, exposure to such wavelengths may promote tolerance of the photosystem to other stressful stimuli.

3. Desirable traits in crop production are regulated extensively by UV radiation

Such well-described, yet poorly characterized, alterations in plant form in response to managed UV-B exposure, such as increased leaf thickness and enhanced photoprotection, could make a substantial contribution to a crop plant's ability to tolerate such myriad combinations of stress. There are certainly growing indications that photosynthetic outputs could be positively regulated via exposure to biologically realistic levels of UV-B (Table 1), and our understanding of the underlying concepts related to UV-mediated growth enhancement is now expanding. For example, the exposure of young *L. sativa* seedlings to ambient UV-B levels at a mid-northern latitude, far earlier in the crop developmental cycle, led to eventual yield increases of 29% on harvest (Wargent *et al.*, 2011). The authors noted increases in net photosynthetic rate during the early stages of enhanced UV-B exposure, and also observed indications that early exposure to UV-B may provide photoprotective benefits before plants are transplanted into field conditions. Limits to photosynthetic efficiency are seen as crucial bottlenecks in increasing crop productivity (Parry *et al.*, 2011), and delays in the recovery of the photosystem from a 'photoprotected' state, when faced with excess light, back to a high-efficiency state commonly lead to decreases in daily canopy carbon gain (A_c); for example, Zhu *et al.* (2004) estimated that the costs of a delayed recovery from photoprotection to be a 17–32% reduction in A_c depending on ambient temperature and genotype. Equally, plants with enhanced photoprotective traits, or recovery ability from photoinhibition, are likely to gain overall productivity advantages in high-PAR situations (Zhu *et al.*, 2010). Frequently, the photosynthetic capacity of a plant may be observed oversimplistically on the basis of single-time-point studies, but carbon assimilation is integrated across the entire life cycle and canopy of a cultivated crop (Parry *et al.*, 2011), meaning that early net gains in photosynthetic rate, even if employed in photoprotective responses (e.g. on field transplantation), could provide an effective buffer against losses in

Table 1 Examples of beneficial outcomes of exposure to ultraviolet radiation for factors related to plant productivity and stress tolerance

Species	UV dose	Response	Reference
<i>Cucurbita maxima</i>	Field, 60°N	UV-mediated protection from photoinhibition in field-grown crops	Hakala-Yatkin <i>et al.</i> (2010)
<i>Fagopyrum tataricum</i>	6.3 kJ m ⁻² d ⁻¹ UV-B _{BE}	Yield increased in 2 populations (/15 total)	Yao <i>et al.</i> (2007)
<i>Glycine max</i>	5 kJ m ⁻² d ⁻¹ UV-B _{BE}	SOD activity increased in 10 cultivars (/20 total)	Zu <i>et al.</i> (2003)
<i>Gracilaria lemaneiformis</i>	Field, 35°N	UV-A enhanced relative growth rate (RGR), UV-B decreased RGR; UV-B mediated F_v/F_m recovery following UV-led reduction	Xu & Gao (2010)
<i>Hippophae rhamnoides</i>	5.3–8.5 kJ m ⁻² d ⁻¹ UV-B _{BE}	Modest increase in photosynthetic rate	Yang & Yao (2008)
<i>Hordeum vulgare</i>	10.3 kJ m ⁻² d ⁻¹ UV-B _{BE}	Increased photosynthetic rate in 1 cultivar (/3 total)	Hideg <i>et al.</i> (2006)
<i>Lactuca sativa</i>	Field, 53°N	Earlier UV-B exposure led to increased final yield	Wargent <i>et al.</i> (2011)
	10 kJ m ⁻² d ⁻¹ UV-B _{BE}	Increases in photosynthetic rate, F_v/F_m recovery	
<i>Mentha piperita</i>	0.6 W m ⁻² *	Elevated monoterpenoid oil production in response to high PAR (1150 μmol m ⁻² s ⁻¹) and ambient UV-B as compared to low PAR (550 μmol m ⁻² s ⁻¹) and no UV-B	Behn <i>et al.</i> (2010)
<i>Oryza sativa</i>	Field, 38°N	Increased grain nitrogen content	Hidema <i>et al.</i> (2005)
<i>Oryza sativa</i>	9.7 kJ m ⁻² d ⁻¹ UV-B _{BE}	Increased photosynthetic rate, increased tolerance to photoinhibition	Xu & Qiu (2007)
<i>Pseudotsuga menziesii</i>	6 kJ m ⁻² d ⁻¹ UV-B _{BE}	Photosynthetic rate 32% higher in UV-B acclimated seedlings following 4 d of exposure to elevated PAR	Poulson <i>et al.</i> (2002)
<i>Triticum aestivum</i>	5 kJ m ⁻² d ⁻¹ UV-B _{BE}	Increased stomatal conductance and transpiration in three cultivars (/10 total)	Li <i>et al.</i> (2010)
<i>Triticum aestivum</i>	5 kJ m ⁻² d ⁻¹ UV-B _{BE}	Increased 'quality response index' in 9 cultivars (/10 total); 5 cultivars exhibited increased protein content	Zu <i>et al.</i> (2004)

Responses detailed above are examples and do not convey the entirety of the study findings.

Field, field exposure to local solar UV radiation; F_v/F_m , quantum efficiency of photosystem II; PAR, photosynthetically active radiation; SOD, superoxide dismutase; UV-B_{BE}, biologically weighted UV radiation (Caldwell, 1971).

*No biological spectral weighting function used in UV dosimetry.

total plant assimilation endured during and following transplantation, leading to increased yields, such as those observed above (Wargent *et al.*, 2011). The UV-B growth inhibition response has frequently been described as a negative consequence of UV exposure in crops and other species, particularly with regard to reductions in leaf number and reduced growth rates (Krizek *et al.*, 1998). Yet, for example, concomitant increases in leaf thickness may compensate for such losses of leaf area via increased RUBISCO concentration per unit leaf area, a trait previously observed in dwarfing wheat genotypes (Morgan *et al.*, 1990). Indeed, enhanced photosynthetic ability as a consequence of such related trade-offs has been suggested by other authors as an indirect outcome of the UV growth model caused by a total increase in leaf volume (Yang & Yao, 2008). For example, a reduction in radiation use efficiency in larger or rapidly expanding leaves as a result of the carbon re-consumed by respiration to support shaded growth has been observed in various systems (Murchie *et al.*, 2009), and the interplay of UV-B morphogenesis may be a valuable factor in this respect. An answer to the question of whether a UV-mediated compaction of leaf development or canopy growth habit leads to a long-term penalty or benefit for plant growth remains somewhat elusive, and exposure timings, duration and developmental stage are key considerations. For example, Wargent *et al.* (2011) demonstrated that relative growth rates increased in young *L. sativa* plants continuously exposed to UV-B for a total period of 26 d; yet, conversely, sudden exposure to the same dose of UV-B for only the final 10 d of the same period limited plant growth drastically by comparison. One limiting factor in studies to date is

certainly the consistent reliance on spot leaf measurements of assimilation as opposed to assessments of whole-plant gas exchange, together with the possible variation in growth outcomes on a species-to-species basis. Although there is still much work to be done regarding mechanistic understanding, the concept of increased crop stress tolerance as mediated by UV-B could arguably present a valuable future exploitable outcome of UV photomorphogenesis in modern agriculture.

The enhancement of crop nutritional qualities has been a long-pursued endpoint of plant biology, including both genetically modified approaches and other breeding-led methods (Parr & Bolwell, 2000; Niggeweg *et al.*, 2004). The known contribution of beneficial phytochemicals to a healthy diet (Surh, 2003) has led to recent speculation that significant increases in plant food product production and consumption may be a key strategy in mitigating against declining human health, and may present an option for establishing adequate global nutrition under threat of climate change (Friel *et al.*, 2009). Given that it is so widely established that UV radiation can up-regulate secondary metabolism in such a marked fashion, it is prudent to consider the contributions that such integral components of UV response may have for food nutrition. Yet, despite the mounting evidence that UV, and UV-B in particular, can act as a basic stimulus to a relatively wide range of metabolite groupings, there remains limited knowledge with regard to what extent we can target and control metabolite responses which then lead to named nutritional outcomes (as reviewed by Jansen *et al.*, 2008). Downstream outcomes of the key phytochemical response to UV radiation, that of the phenylpropanoid

pathway, and the flavonoids and hydroxycinnamic acids in particular, have been clearly associated with perceptible health benefits on a general basis for some time (Harborne & Williams, 2000; Stintzing & Carle, 2004), yet the complete association between defined UV exposure, the generation of specific metabolites and measured human health benefits remains elusive, largely as a result of knowledge gaps regarding the trade-offs across multiple-UV-wavelength signal transduction pathways for particular metabolite production. For example, Kotilainen *et al.* (2008) demonstrated that, within a group of 20 leaf phenolic compounds isolated from alder and birch trees, some compounds were affected equally by UV-B and UV-A exposure, some compounds responded in opposite directions to the two different wavebands, and some compounds simply did not respond to any great extent at all to UV. Equally elusive are the notoriously challenging characterizations of the underlying human biology in response to increased intake of such phytochemical compounds (Halliwell, 2007), yet good models now exist on, for example, berry fruit composition and enhanced recovery from exercise-induced muscle damage (McLeay *et al.*, 2012). Nonetheless, there remains significant potential for the utility of UV exposure as a regulator of plant 'neutraceutical' content, with a range of compounds observed to respond favourably to UV radiation, including the antioxidants (Kähkönen *et al.*, 1999; Costa *et al.*, 2002; Agarwal, 2007), alkaloids (Ramani & Chelliah, 2007) and glucosinolates (Reifenrath & Müller, 2007), although, often, there is reported variation in terms of compound regulation by UV. One metabolite notably associated with benefits to health is the phytoalexin 3,5,4'-trihydroxystilbene, commonly known as resveratrol, which, despite some debate, has been routinely shown to inhibit cancer development and to possibly contribute towards therapies for obesity and ageing disorders in animal systems (Jang *et al.*, 1997; Baur & Sinclair, 2006; Baur *et al.*, 2006). Resveratrol is known to be commonly isolated in high concentrations from the skins of red grapes (Moreno-Labanda *et al.*, 2004), and there is now good evidence that a key precursor to resveratrol biosynthesis, stilbene synthase, is up-regulated at a transcriptional level in response to UV, in addition to resveratrol content itself (Pan *et al.*, 2009; Tang *et al.*, 2010; Wang *et al.*, 2010), although such responses have commonly been elicited with the use of UV-C wavelengths in the majority of studies to date, providing a certain amount of speculation as to whether resveratrol can be consistently produced by UV-B *in planta* under natural sunlight. There are certainly reports that exposure to solar UV-B can alter the taste of leafy vegetables, leading to a more 'bitter, intense' taste (Paul *et al.*, 2005), and this is most likely a reflection of alterations in plant chemistry and other aspects of morphology. Notably, there is a great deal of information regarding the possibilities of exploiting the UV response at the post-harvest phase of crop production (Allende *et al.*, 2006; Lemoine *et al.*, 2007), typically via the use of short-wavelength (i.e. UV-C) supplementary lighting, further underlining the possibilities which may be unlocked by an increased understanding of UV response in the field. One likely crucial aspect of the exploitation of the UV phytochemical response is that of exposure timing; it is known that committed steps in phenylpropanoid metabolism, such as transcription of *CHS*, can be up-regulated within minutes of UV-B

exposure (Jenkins, 2009), yet the elicitation of flavonoid compounds can be highly dependent on the developmental stage. For example, grapes are historically cultivated in high-UV environments, yet the accrual of phenolic pigmentation often only occurs after the berry-ripening (or veraison) stage of development (Gregan *et al.*, 2012), despite the fact that developing berries have been exposed to UV radiation for a considerable time before this phase, and typically at seasonally higher incident UV fluxes than those encountered post-veraison. This may be accounted for by timed regulation of the biosynthetic pathway, whereby the biosynthesis of stilbenes (e.g. resveratrol) is known to take place up to veraison, with flavonoid biosynthesis typically increasing after veraison. Although these biosynthetic pathways possess common components, post-veraison sunlight induces the transcriptional regulation of anthocyanin and flavonol synthesis in berry skins (Czemmel *et al.*, 2009), thus suggesting that the consideration of a crop's temporal response basis is frequently underexplored because of the commonality of single-time-point experimental studies. Equally, related aspects of UV photomorphogenesis, such as cellular and tissue-based localization of metabolites, are also key components of building a working model for optimal UV exposure for particular outcomes. Therein lies an inherent trade-off between differing components of UV metabolite response, and the building of our understanding of how discrete and overlapping regulatory components drive specific outcomes in plant physiology and chemistry should be a crucial future consideration in combining the UV response of desired traits in crop plants together with an appropriate genotype.

4. Modern crop production systems provide significant opportunity to regulate the UV environment

It could be argued that the semi-ubiquitous nature of UV radiation provides limited scope for enhanced utility within modern crop production, largely because of the perceivable difficulties in manipulating the UV environment, particularly for crops that are grown in the field throughout their lifetime. Yet, currently, more potential exists than ever before for the use of UV radiation as a cue to induce desirable endpoints in crop yield and other indicators of food plant prosperity (Table 2), and such potential arguably extends across most, if not all, cropping environments. It is clear that species and cultivars can exhibit marked differences in UV response and, as with other environmental cues, an understanding of genotypic sensitivity to UV radiation is a key aspect in driving enhanced crop resilience. For example, there is currently limited information regarding the degree of conservation of key signal transduction pathways to UV-B across a variety of crop species, but it is now known that several higher plant species possess protein sequences with marked similarities to the UVR8 locus (Jenkins, 2009). In more general terms, an inevitable consequence of genotypic variation is variation in plant architecture, thereby potentially exposing plants to more or less UV-B, and the selection of cultivars which orientate in a manner that may allow for prediction-based exploitation of beneficial UV-mediated outcomes is arguably a key determinant of UV response. For example, He *et al.* (1993) noted that monocotyledonous species, with their erect

Table 2 Desirable traits in crops which may be regulated by UV radiation

Crop type	Desired outcome
Cereal crops	Breeding for manipulation of UV-photomorphogenesis Cultivar-selection for optimisation of photosynthetically efficient plant architecture
Rice	Increased photosynthetic productivity Increased photosynthetic efficiency
Tuber crops	Enhanced nutritional quality of harvestable components
Vegetables	Plant growth regulation Reduced losses from field transplantation
Vegetables, fruits	Improved taste, colour & shelf-life Post-harvest treatment for enhanced nutritional benefits/food safety
All crops	Deterrence of insect pest feeding (e.g. herbivory) Efficient management of beneficial insects (predators, parasitoids, pollinators) Plant pathogen control (e.g. induced plant resistance, direct mortality)

The possible exploitation of such attributes requires a robust means to deliver UV radiation to the target crop via managed exposure during a crop production life cycle, and/or the availability of biotechnological tools; for example, breeding for the manipulation of UV response is a longer term goal, whereas enhancement of vegetable taste and colour is already feasible via the deployment of spectral filters (Section II.4 Modern crop production systems provide significant opportunity to regulate the UV environment).

form, do not seem to be as responsive to UV-B as dicotyledonous species, with more horizontal lamina, although there is a paucity of studies in which direct comparisons have been made. At the same time, there are notable examples in which an increased photosynthetic rate has been observed in a range of studies focused on monocotyledonous species, including wheat, barley and rice (Table 1). Leaf architecture on an interspecific and intraspecific basis is also highly likely to influence the nature of UV-B penetration to underlying tissue, and this may drive any dichotomy between plants which may be more responsive to UV photomorphogenesis and those which may be less sensitive. In much the same way as the current extensive attention given to the optimal plant architecture for the maximization of total plant photosynthetic capability (as reviewed by Zhu *et al.*, 2010), it would be prudent to extend our understanding of the regulatory effects of UV on architectural development. For example, alterations in leaf angle and dwarf habit caused by loss of function of the brassinosteroid insensitive1 orthologue OsBRI1 have been associated with higher grain yields in rice (Morinaka *et al.*, 2006); interestingly, there are now early-stage indications that brassinosteroid activity may contribute to the UV-B growth response (Hectors *et al.*, 2007). In terms of the other factors which may affect incident UV reaching a crop, principally in outdoor systems, but also in protected environments, site selection frequently encompasses such decision-making factors as topography and solar aspect in relation to adequate photosynthetic radiation. Optimization for sunlight exposure in this manner inevitably influences UV flux, and has the potential to alter morphogenic responses (Rousseaux *et al.*, 2004). Furthermore, in contrast with a natural ecosystem, modern crop production is an intensive process and, in addition to factors such as

cultivar selection and cropping density (as discussed by Ballaré *et al.*, 2012), crop manipulation techniques, such as pruning and leaf removal, are intrinsic within agriculture, and this allows further potential to maximize UV perceptivity for a desired attribute. For example, the cultivation of perennial crops often requires an elevated level of canopy and vigour management, and systems such as grapevine and other perennial fruit crops have been subject to a continuing level of biotechnological innovation to achieve maximal productivity over time (Vivier & Pretorius, 2002). In addition, ground-laid reflective films are now used routinely in temperate growing regions in order to reflect light into the canopy to achieve pigmentation induction in developing fruit (Prive *et al.*, 2008). The expansion of whole-genome sequencing in commonly cultivated crops can only add to the possibilities for managed, productive interactions between genotype and UV environment (Jaillon *et al.*, 2007; Velasco *et al.*, 2010), via exploitation of the UVR8 locus for example.

Protected cultivation is a key aspect of modern agriculture, with cropping systems devoted to protecting crops under glass or via the use of other protective structures expanding *c.* 20% yr⁻¹ on a global basis from a previous share of *c.* 7% of the total vegetable production area in developed countries in the mid-1990s (Jensen & Malter, 1995; Espí *et al.*, 2006). Although limits to the exploitation of UV photomorphogenesis in crops grown outdoors for the majority of their life cycle may at first appear to be significant, *c.* 50% of the world's crops are probably produced via 'field transplantation', whereby seedlings are initially propagated in a protected environment and then transplanted into the field, and there are already clear indications that early-stage enhancements of the UV environment may lead to an increase in crop productivity following field transplantation (Wargent *et al.*, 2011). In addition, the expansion of food production into increasingly challenging environments, often encountering high temperatures and low water availability, inevitably overlaps with latitudinal locations that are subject to comparatively higher UV fluxes, yet, arguably, even in geographical locations which are not subject to the extremes of UV radiation, there exists equal potential for the manipulation of UV photomorphogenesis. The increasing use of polyethylene-covered protective structures has been a significant contributor to the expansion of protective crop management, and recent developments in polymer technology are providing protective filters which can manipulate or selectively filtrate elements of incoming electromagnetic radiation, including the infra-red for temperature control (García-Alonso *et al.*, 2006), the red : far-red spectrum as mediated by phytochrome (Runkle & Heins, 2002) and, more recently, the UV spectrum (Paul *et al.*, 2005), whereby differing elements of the UV spectrum can be included or excluded from incident radiation. The use of such technology has already been highlighted as one technique which could make a marked contribution to food security in the future (The Royal Society, 2009), yet further studies are needed to evaluate the trade-offs of UV exposure. For example, although a UV-inclusive environment may be valuable to enhance plant phytochemical content, there may be complex implications for disease control (Paul *et al.*, 2012) (see Section III UV influences a wide range of agro-ecosystem interactions with plants and other biota).

The use of artificial sources of photosynthetic radiation is a significant component of modern crop production, yet recent advances in semiconductor technology have also provided sharp possibilities for the exploitation of UV response using artificial lighting indoors, and there is already some evidence that the use of supplementary UV-B can regulate crop growth, enhance foliar colour and induce fungal disease resistance (Wargent *et al.*, 2006). In the past, there has been relatively limited scope to modify the light spectrum because of physical constraints of the sources available. However, the advent of next-generation light-emitting diodes (LEDs) is likely to herald a new age in photomorphogenic manipulation, whereby the wavelength specificity of light sources is set to increase dramatically, unlocking the exploitable possibilities of plant response, such as tailoring lighting environments to UVR8-mediated photomorphogenesis, for example. Indeed, the potential of LED technology to deliver desirable outcomes in protected crops is now being investigated (Brazaityte *et al.*, 2010), but with some progress yet to be made. In summary, there exists a range of possibilities to modify the UV environment for the enhanced exploitation of desirable photomorphogenic response, including trait targeting for optimal photomorphogenic response via breeding and cultivar selection, the use of early-stage modified UV regimes for field crops before field transplantation, plus 'follow-on' field manipulations of UV radiation using tools already partly incorporated into cultivation practice in many parts of the world.

III. UV influences a wide range of agro-ecosystem interactions with plants and other biota

Plants are not alone in their perception of and sensitivity towards UV wavelengths, and the diverse multi-biotic nature of global agro-ecosystems continues to pose challenges for crop production, largely as a consequence of the 'moving target' of pest and disease attack. Actual losses attributed to the varied impacts of pest and disease have been estimated at 26–40% for sugar beet, barley, soybean, wheat, cotton, maize and rice (Oerke & Dehne, 2004), with potential losses estimated by the same authors at 50–80% across selected key crops. It is also widely believed that pest and disease pressures may be exacerbated by climatic change (Percy *et al.*, 2002; Jump & Peñuelas, 2005). Many of the diverse and dynamic aspects of plant photomorphogenesis are composed of physical and chemical endpoints which are commonly associated with pest and disease resistance, thus indicating an enhanced and as yet underexplored role for UV radiation within integrated pest and disease management strategies (Paul & Gwynn-Jones, 2003; Mazza *et al.*, 2012). The role of plant secondary metabolism as a constitutive and inducible defence against insect feeding has been characterized extensively (Baldwin *et al.*, 2001; Kliebenstein, 2004), and the development of such defences as a key plant strategy to deter pest foraging and/or reduce palatability could be considered as an exaptation of the UV phytochemical response, developed against the transition of plants from water to land in a background of high UV flux. In a similar manner to the aforementioned commonly observed aspects of plant UV photomorphogenesis, deterrence in insect pest feeding or attack on plants

exposed to UV-B is now a frequently observed phenomenon (Ballaré *et al.*, 1996; Lindroth *et al.*, 2000; Rousseaux *et al.*, 2004), with the majority of observations based on feeding choice experiments carried out under field conditions using selective solar UV filtration, or in the laboratory, with a common focus on the Lepidoptera. Despite the generalized correlation between UV exposure, induction of secondary metabolism and consequences for pest defences, specific mechanisms have remained somewhat obscure, with past studies highlighting the difficulties in attributing anti-feedant responses to particular UV-induced metabolites (Hatcher & Paul, 1994); yet, progress is now being made. For example, significant convergence in the composition of phenolic response to both UV-B and stimulated herbivory has been demonstrated in the model system *Nicotiana*, with chlorogenic acid and dicaffeoylspermidine isomers the commonly associated responders to both stimuli (Izaguirre *et al.*, 2007); interestingly, the key flavonoid observed during the study, rutin, was singularly induced by UV-B and not herbivory. The identification of signalling initiators and intermediates in the UV–herbivory response presents a desirable aim, and it has been hypothesized that the key signalling component of the wounding response, jasmonic acid (JA), could be a primary regulator. In support of JA as a mediator of UV-induced plant defence, adult moths were observed by Caputo *et al.* (2006) to preferentially deposit eggs on plants which had not received supplementary UV-B exposure, yet this deterrence effect was diminished in plants with the *jar1-1* mutation, which were hence deficient in JA signalling. Furthermore, silencing of the lipoxygenase-3 (LOX3) gene in *Nicotiana attenuata* plants led to greatly reduced UV-B-mediated resistance to insect attack in the field and, despite no observed increase in endogenous JA levels in wild-type plants, increased sensitivity of jasmonate-responsive genes, such as trypsin proteinase inhibitor (TPI), occurred in response to UV-B (Demkura *et al.*, 2010). Thus, a pattern is emerging whereby the role of UV-B in pest resistance is not driven in its entirety by particular signalling pathways or the elicitation of specific secondary metabolites, such as the flavonoids, for example. Further progress is needed to elucidate the role of UV photomorphogenic signalling cascades in the regulation of the herbivory response (i.e. UVR8–COP1–HY5), yet there are early indications that UVR8 may form an element of plant herbivore defence. For example, Fig. 2(a) summarizes a herbivore choice study in which the generalist *Spodoptera littoralis* preferentially selected *uvr8* mutant plants rather than wild-type plants, following early propagation in the absence of UV-B (Fig. 2a). It is clear that the absence of UVR8 function in the mutant may result in certain constitutive differences in phenotype; for example, referring again to the study by Favory *et al.* (2009), a comparison of gene expression in *uvr8* plants relative to wild-type plants in the absence of UV-B indicates significant up-regulation of several functional gene categories regulating cell wall processes (Supporting Information Table S1) and the down-regulation of a selection of RNA transcription and DNA synthesis gene groups. When *uvr8* and wild-type plants were then exposed to a high, but globally realistic, UV-B dose for just 12 h, *S. littoralis* larvae exhibited no significant preference for either genotype, indicating a declining preference for *uvr8* plants (Fig. 2a). It is probable that the higher UV-B dose

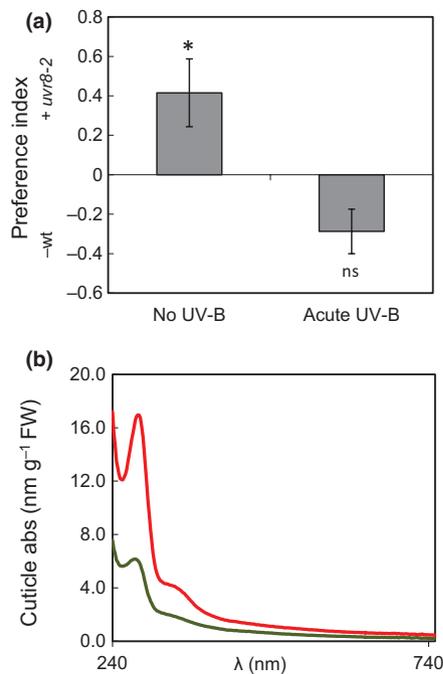


Fig. 2 UV-B plant response leads to diverse consequences for insect pest behaviour and development. (a) Feeding choice of the generalist herbivore *Spodoptera littoralis* was assessed in the *Arabidopsis uvr8* mutant vs wild-type (*wt*, *Ler*). Following germination and within a background of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ white light, *uvr8-2* and *wt* plants were maintained for 28 d (No UV-B), and 28-d-old *uvr8-2* and *wt* plants were exposed to a high dose of biologically effective UV-B radiation ($\text{UV-B}_{\text{Caldwell}} = 10.0 \text{ kJ m}^{-2} \text{ d}^{-1}$ weighted using the Caldwell generalized plant action spectrum) for 12 h (Acute UV-B). Pre-starved pairs of third/fourth instar *S. littoralis* were then introduced to isolated pairs of equal sized *uvr8-2* and *wt* plants for a period of 300 min. Defoliation of leaf material was characterized via image analysis of plant rosette leaf area, with the Preference Index (PI) calculated as $\text{PI} = (X - Y)/(X + Y)$, where X is the leaf area consumed of *uvr8-2* plants and Y is the leaf area consumed of *wt* plants, with $\text{PI} = 1$ or $\text{PI} = -1$ indicating full preference for *uvr8-2* plants or *wt* plants, respectively. Asterisk indicates significance from PI of zero at $P < 0.05 \pm 1\text{SE}$ (ns, not significant). Ten paired choice assays were carried out per experiment (i.e. with No UV-B mutant/*wt* pairs, and with Acute UV-B mutant/*wt* pairs), and the results presented are from four individual experiments. (b) Cuticular absorbance of the generalist herbivore *Epiphyas postvittana* was characterized following a forced diet of UV-B-treated *Lactuca sativa* foliage (no UVB, green line; UVB+, red line). Twenty-one-day-old *L. sativa* plants were exposed to a $\text{UV-B}_{\text{Caldwell}}$ dose of $10 \text{ kJ m}^{-2} \text{ d}^{-1}$ for 7 d (UVB+) alongside control plants that did not receive UV-B (No UVB). Following irradiation, the third true leaves of the plants were defoliated and offered to fourth instar *E. postvittana* larvae according to the individual treatment for a period of 48 h. The insects were then eviscerated and the cuticles were homogenized in acidified methanol before spectrophotometric analysis. Each line shown according to UV treatment is the mean of five individual cuticles.

employed in this element of the study may have led to the expression of UVR8-independent responses in the *uvr8* mutant, as indicated by the parallel induction of several functional gene groups in the *uvr8* mutant and wild-type in the study by Brown *et al.* (2005) discussed earlier. The regulatory effects of UVR8-specific UV-B photomorphogenesis on herbivory defence are yet to be fully characterized, but this example suggests further that our knowledge is still very much limited regarding the possible overlaps between

UVR8-dependent and acute UV-B signalling in the context of varied field UV-B fluxes. In recent years, the prominence of strategies, such as Integrated Pest Management (IPM), to achieve sustainable routes forward in crop production has received a great deal of attention (Vet & Dicke, 1992; Cook *et al.*, 2007), with the use of the biological control of crop pests with natural enemies, for example, insectivorous parasitoids and predators, rapidly becoming a vital component of agronomic practice. Although the consequences of the UV-B plant response for herbivore feeding are now fairly well established, there is still little information regarding the knock-on effects for higher trophic interactions. There is, however, an intriguing indication that UV-B exposure may mediate yet further desirable endpoints in crop protection; Foggo *et al.* (2007) showed that, during a series of choice experiments, *Cotesia plutellae*, a parasitic wasp of the diamondback moth (*Plutella xylostella*), was attracted to brassica plants which previously had been exposed to supplementary UV-B, thus indicating some potential for UV-led trophic interactions in the context of pest control. Although the same study also indicated that moth larvae raised on a diet exclusively composed of UV-B-exposed plant tissue were subject to reduced weight gain by the completion of the larval phase of development, insect foragers may be subject to trade-offs in terms of positive and negative outcomes of consuming UV-B-exposed plants. For example, Fig. 2(b) shows the cuticular UV-absorbing compound content of the generalist herbivore *Epiphyas postvittana* following larval feeding on *L. sativa* leaves which were subjected to UV-B exposure. Here, exclusive feeding on UV-B-treated leaves led to increased cuticular absorbance across the UV spectrum, indicating the possibility of additional physiological consequences for herbivores as a result of UV photomorphogenesis, for example photoprotection, and insect health. In terms of the sensory interactions that influence insect foraging, yet are not directly related to feeding, there is currently little information regarding the influence of UV exposure on plant-emitted volatile compounds which often influence insect decision-making, although it is clear that longer wavelength UV, such as the UV-A waveband, is a common component of insect vision, and the use of UV-inclusive and UV-exclusive filters has shown that the UV environment does regulate visual-based behaviour by insect pests (Antignus *et al.*, 2001). Interestingly, although evidence is limited, the role of UV-B wavelengths in insect vision has also been demonstrated recently (Mazza *et al.*, 2010). Arguably the most significant role of 'beneficial' insects within an agro-ecosystem is pollination, with the value of pollination as an ecosystem service estimated at $\$117 \times 10^9 \text{ yr}^{-1}$ based on 1997 values, with more than one-third of the total value of pollination attributable to croplands (Costanza *et al.*, 1997). It is known that insects, such as bees, use UV radiation as a visual cue, yet we know little regarding a direct association with UV photomorphogenesis, inflorescence morphology and pollinator interaction, although there is evidence that UV can influence floral development and may regulate pollinating insect interest as a consequence (Petropoulou *et al.*, 2001; Koti *et al.*, 2005).

Plant pathogen responses to UV radiation remain poorly characterized at a mechanistic level, particularly in terms of understanding the wavelength and dose dependence of the

various signal transduction elements involved, with many past studies again focused on unnaturally high UV fluxes. An intriguing prospect of UV-response manipulation for disease control lies in the variability of differing, yet proximate, wavebands in eliciting quite different patho-responses. For example, it is quite well established that the exposure of fungal pathogen spores to UV-B radiation will result in spore death (Paul, 2000; Wu *et al.*, 2000; Paul *et al.*, 2005), almost certainly as a consequence of chronic damage, yet UV-A wavelengths are known to stimulate the sporulation of some pathogens, as has been demonstrated using UV-excluding filters (Elad, 1997). When combined with our understanding of the role of blue light in suppressing the development of some fungi (Reuveni & Raviv, 1997), a somewhat complex picture emerges, yet modification of the light environment of a crop with disease control in mind is fully conceivable (Raviv & Antignus, 2004; Vanninen *et al.*, 2010), and would need to take into account local UV fluxes and spectral balance in order that particular pathosystem responses are targeted effectively. This was demonstrated by Paul *et al.* (2012), who noted that not only did crops at a mid-northern latitude exposed to a fully UV-inclusive and UV-opaque environment express parallel reductions in infection by *Bremia lactucae* and *Botrytis cinerea*, but that, *in vitro*, UV doses required for a 50% reduction in spore germination varied quite markedly between pathogen and phylloplane organisms. In an equal sense to that of insect resistance, the question of host resistance could be a prominent aspect of the UV–pathogen interaction. Plant responses to pathogen attack remain a much explored topic in plant biology (Glazebrook, 2005; Jones & Dangl, 2006), yet there is currently very little information regarding the involvement of the well-defined plant resistance networks in UV-mediated host resistance. However, there are indications that pre-exposure to UV-B subsequently induces resistance to fungal infection at a time point after exposure has ended (Wargent *et al.*, 2006), and that such resistance may be mediated by UVR8 via controlled expression of sinapate compounds (Demkura & Ballaré, 2012). There are additional considerations for the impact of the UV environment beyond pathogens which infect plants; fruit and vegetables are now thought to be a significant source for the introduction of food poisoning bacteria into the food chain (Berger *et al.*, 2010). The use of germicidal, short-wavelength UV has been evaluated for postharvest exposure of fruit and vegetables and water treatment techniques (Chen *et al.*, 2009), and yet, although many food pathogens, such as *Salmonella* sp., can readily survive on growing plant surfaces, there is little information regarding the consequences of UV morphogenesis for human pathogen survival and growth; for example, the role of the phylloplane in protecting leaf-harboured pathogens from the direct or indirect effects of UV exposure has been little explored. In summary, UV radiation exerts a vast range of influences on diverse biota, including herbivorous and other insect pests and plant pathogens, and there is the potential to greater inform pest and disease control, in addition to managing beneficial agronomic biota, more effectively through an understanding of the UV response.

IV. UV interacts with many abiotic processes within a global agro-environment

Climatic perturbations are likely to lead to interactions with UV radiation and other environmental factors at a previously unseen level in the future, with mounting significance for crop cultivation. For example, it is believed that warming global temperatures could lead to upper limitations in the adaptive capacities of crops grown at low latitudes (Easterling *et al.*, 2007). It is well established that UV-B responses are certainly influenced in combination with other environmental parameters, yet few studies to date have provided mechanistic insight into such interactions. PAR, water availability, temperature, pathogen infection and many other abiotic stress factors are known to modify the UV-B response (Jordan, 1996; Mackerness *et al.*, 1996; Logemann & Hahlbrock, 2002; Caldwell *et al.*, 2003), and the diverse range of observations to date are most likely a consequence of variations in UV treatment methodology and timing of co-factor application (Deckmyn *et al.*, 1994; Flint *et al.*, 2009). The prospect that simultaneous adaptive advantages may be conferred by UV-B exposure when encountering other abiotic factors clearly requires further investigation, yet there are indications that elevated CO₂ may provide photosynthate and/or other ‘compensatory’ benefits for the growth of UV-B-exposed plants (Qaderi & Reid, 2005; Koti *et al.*, 2007).

UV radiation also potentiates various other photochemical processes of agronomic significance. There is increasing scrutiny with regard to the level of agrochemical deposition on fruit and vegetables, largely as a consequence of concerns regarding human health (Goldman & Koduru, 2000). Photodegradation of chemicals by sunlight is known to act as a substantial driver for reduced chemical persistence in water, and on soil and plant surfaces (Ciani *et al.*, 2005; Nadal *et al.*, 2006). It has been demonstrated that UV wavelengths are involved in the photodegradation of agrochemicals, and that enhanced UV inclusion within cropping systems, such as protected cultivation, could present an additional means by which chemical contamination of foodstuffs could be mitigated (Weber *et al.*, 2009a,b). Furthermore, the extended role of UV radiation as a regulator of photochemical processes has been recently augmented by the observations of methane (CH₄) production from foliar pectins as induced by UV (McLeod *et al.*, 2008). Despite estimations of the contribution of global CH₄ emissions from vegetation foliage appearing to be substantially lower than first thought (Bloom *et al.*, 2010), the contribution of UV to such processes warrants future consideration. Large-scale processes which are of current marked importance to agriculture also include carbon cycling, whereby increased carbon sequestration in agricultural landscapes could represent a significant contribution to efforts to limit the atmospheric deposition of CO₂ (Sauerbeck, 2001). Moreover, there has been recent debate as to the possibilities presented by bio-engineering for increased vegetative albedo as a contribution to the mitigation of rising global temperatures (Ridgwell *et al.*, 2009), largely via the selection of specific traits within agricultural crops, such as leaf waxiness. The ability of UV to up-regulate leaf wax content may be worthy of further investigation as a possible route to enhance the likelihood of such large-scale attempts to mitigate global challenges, such as

increased temperatures, and may offer a route to regulate plant water use efficiency (WUE).

V. Conclusion: can we exploit UV photomorphogenesis in agriculture?

UV radiation imposes a significant influence over numerous aspects of modern agriculture (Fig. 3). There have been a significant number of studies to date which have described negative implications of the UV response for plant development, yet numerous studies have frequently used unbalanced spectral manipulations, unrealistically high supplementary fluxes and/or *in vitro* exposures of single cellular components. This has brought a certain amount of confusion to the overall perception of UV radiation as a stimuli of plant development, yet significant questions remain with regard to the fuller consequences of UV radiation for agro-ecosystems and other ecological systems, and such uncertainty may be further

perturbed by future climatic change. Therefore, more focused experimental approaches continue to be extremely valuable in building our understanding of photomorphogenesis, and there is still limited understanding of the regulatory processes which govern many aspects of the UV–plant response, from signal transduction through to such outcomes as the induction of protective compounds or reductions in leaf expansion. The use of biological spectral weighting functions provides a valuable tool for the development of our understanding of the UV-mediated plant response on a wavelength and flux-dependent basis, a crucial aspect in the scaling from experimental conditions to other environments. The need for the increased prediction of desirable and undesirable agronomic outcomes of UV photomorphogenesis is significant and, with the uncertainty of global UV-B fluxes set to remain throughout this century, UV radiation remains an environmental factor of importance. Complementing cultivation systems with the prior selection of cultivars or lines which may respond favourably to the local UV environment is arguably crucial in monopolizing the UV response for desirable endpoints in a changing climate, as is the development of overexpression or silencing tools related to key UV-B signalling components.

Plant biology currently stands at the gateway to a next great revolution of informed stress exploitation for crop productivity and nutrition. At the very crux of the utilization of scientific advance for agronomic gain lies an inherent trade-off between acclimation and chronic shock exposure to environmental stimuli, and many of the debilitating responses mediated by UV wavelengths can arguably be ameliorated or reduced via managed, acclimated exposure to sunlight. This suggests that, from a crop productivity perspective, greater understanding with regard to fundamental responses to UV, such as photomorphogenesis under natural sunlight conditions, will empower efforts to exploit UV-B responses in the utility of producing stress-tolerant quality crops. There is currently little understanding of how differing modes of response to UV-B orchestrate under natural conditions, understandably so, for these are challenging experiments. Nonetheless, as has been the case in the larger scale study of responses to enhanced CO₂, it is vital that efforts to understand the full implications of the UV-B response in a changing climate encapsulate the full balance of natural conditions, yet also provide information regarding fundamental mechanisms, as it is often only under natural conditions that the sum of all parts of the UV-B response can be observed, taking photoprotection as a primary example. As technological innovation advances and the use of differing high-technology, sustainable modes of crop production increases globally, it is time to consider that an energetic environmental cue, such as UV-B radiation, should take its place next to other phenomena which are seen to provide profound influences on crop production and related ecosystems. Enhanced multidisciplinary efforts in key areas of UV photobiology are likely to provide the impetus to achieve valuable steps forward within global food production during this century.

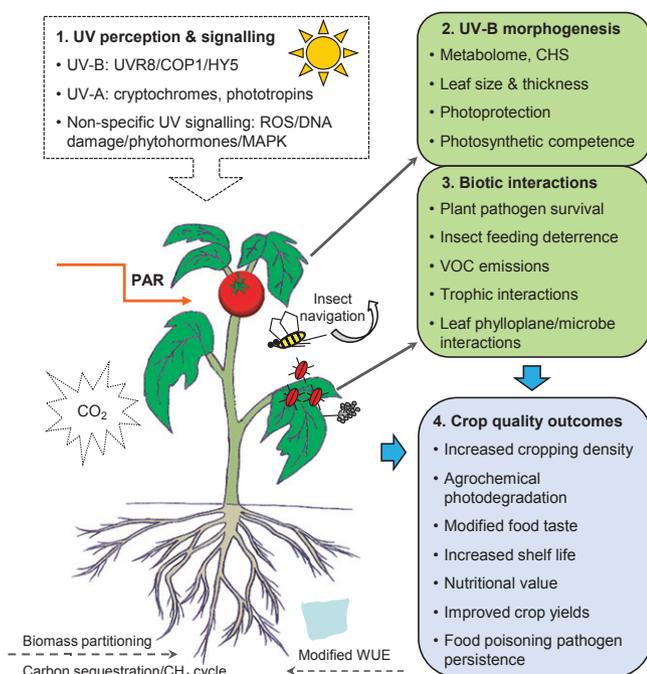


Fig. 3 The UV radiation agro-ecosystem response landscape. (1) Dashed box; UV-B- and UV-A-specific signal perception and signalling (e.g. UVR8), and higher fluence, nonspecific response pathways. Closed arrows indicate outcomes from early-stage responses to UV, including (2) regulation of plant metabolism and morphogenesis, with commonly observed endpoints including leaf growth inhibition and accrual of secondary metabolites, and (3) consequences for related biota, for example deterrence of insect pest feeding, and waveband-dependent effects on plant disease, including direct and host-mediated responses. (4) Blue arrows indicate combined inputs of UV response into hypothesized and observed beneficial endpoints of UV response. The main image highlights the key abiotic factors that influence the UV response, and dashed arrows describe the below-ground and geochemical cycling processes that are influenced by UV–plant interactions. CHS, CHALCONE SYNTHASE; COP1, CONSTITUTIVELY PHOTOMORPHOGENIC1; HY5, ELONGATED HYPOCOTYL5; MAPK, mitogen-activated protein kinases; PAR, photosynthetically active radiation; ROS, reactive oxygen species; UVR8, UV RESISTANCE LOCUS 8; VOC, volatile organic compounds; WUE, water use efficiency.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Summary of MapMan Wilcoxon rank sum test results for all UV-B treatment comparisons from Favory *et al.* (2009) and Brown *et al.* (2005)

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